

SOME FACTORS GOVERNING PLANT DISTRIBUTIONS IN THE MOJAVE-INTERMOUNTAIN TRANSITION ZONE

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ABSTRACT.—The existence of a floristic transition zone can be inferred by the fact that a high proportion of indigenous plant species reach a distributional limit within the area. The vascular flora of Washington County, Utah, exhibits this character to a marked degree with 53.6 percent of the native flora reaching a distributional limit within the county. By looking at geographic distributions, ecological preferences, and range termination information for the component species, first approximations are made as to the probable factors mediating plant distributions within the county, particularly of the range-terminating species. The high proportion of range-terminating species in the flora may be accounted for mainly by limiting factors associated with abrupt shifts along two environmental gradients. The first factor is climatic and is mediated largely by altitude; change occurs primarily along a north-south gradient. The second is both climatic and edaphic and is mediated by factors other than altitude *per se*; it is oriented in an essentially east-west direction. Species with narrower tolerances are shown to be more sensitive to these environmental shifts. Some of the species distributions are better explained by a model involving the effects of interactions between habitat mosaic and genetic homogeneity of given populations on relative migration rates in the transition area. These species may have the capacity to migrate farther, but differences in migration rates give their distributional limits a quasi-stable aspect. These data suggest that species cannot simply be divided into those which are environmentally limited in their present distributions and those which are not. It seems more fruitful to regard these two conditions as extremes on a continuum which can be expressed as migration rate.

A floristic transition zone is characterized by the range termination of a high proportion of the indigenous species. The vascular flora of Washington County, Utah, exhibits this character to a marked degree, with 53.6 percent of the 1,067 indigenous species reaching a distributional limit within the county. The objectives of this study are to obtain detailed documentation of plant distributions within the transition area, to identify environmental factors that might be controlling range limits, and to elucidate relationships between the distribution patterns of groups of species and their ecological amplitude.

Early observations on the floristic transition zone as it occurs in Washington County include those of Parry (1875), Merriam (1893), and Jones (1910). The nature of the

zone as it occurs in Nye County, Nevada, has been examined in some detail by Beatley (1975), while Bradley (1967) has published a phytogeographic survey of Clark County, Nevada, which also lies along the zone. Additional Washington County observations include those of Hardy (1947), Cottam et al. (1959), and Woodbury (1933). Whittaker and Niering (1964) worked with problems of a similar nature in southern Arizona.

DESCRIPTION OF THE STUDY AREA

Washington County is located in the extreme southwestern corner of Utah. It is a roughly rectangular area which spans an east-west distance of about sixty miles and a north-south distance of about forty miles. A

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region of great environmental diversity, the county contains extensive outcrops of carbonate rocks, sandstones, shales, and both extrusive and intrusive igneous rocks (Cook 1960). Elevations range from about 2,000 feet (600 m) near the common boundary with Arizona and Nevada to over 10,000 feet (3100 m) at the top of the Pine Valley Mountains to the north. The dramatic nature of the landscape is exemplified by Zion National Park, most of which lies within the county.

These diverse environments are not mingled randomly; they represent instead the junction and interdigitation of three larger land areas which are themselves relatively homogeneous. Figure 1 shows the geographic position of the county relative to these areas and to the boundaries which separate them.

The first of these boundaries separates the Basin and Range Province from the Colorado Plateau Province. These two areas are very different both lithologically and in the relative proportion of high to low land. The former is comprised of isolated mountain ranges composed mainly of carbonate rocks separated by broad, alluvium-filled valleys. The latter is comprised of a contiguous series of high plateaus composed mainly of sandstone and shale, with lower elevations restricted mainly to relatively narrow canyon floors. The climate of the Colorado Plateau, as a whole, is more mesic than that of the Basin and Range Province. The transition between these two physiographic provinces takes place within the county.

Superimposed on this boundary is another boundary, which is designated on Figure 1 as the 4,000-foot contour line. Valley floors to the north of this line consistently lie above 4,000 feet and thus have a climate which is comparatively cold. Valley floors to the south always lie well below 4,000 feet and thus have a climate which is warmer. The line effectively divides the Basin and Range Province into two subregions, the Great Basin region to the north and the desert lowland region to the south. The fact

that part of Washington County lies south of this line indicates an attenuation of desert lowlands along the Virgin River drainage into an area of generally higher land.

METHODS

The data presented here are summarized from an annotated checklist of the vascular plants of the study area (Meyer 1976). The systems of vegetational and floristic classification used here are more fully explained there.

Each species was assigned to one of thirty-eight floristic groups on the basis of published distributional information. A floristic group is considered as an assemblage of species which share a similar geographic distribution, without historical or ecological implication *per se*.

The floristic groups are here classified into two types of distribution patterns. An areal distribution classification aggregates the floristic groups into five classes on the basis of their areal extent. The directional distribution classification combines the flo-

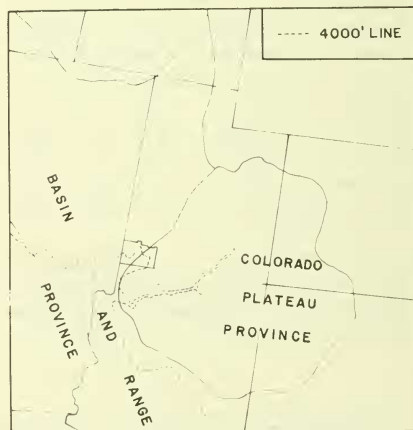


Fig. 1. Location of Washington County, Utah, relative to state and physiographic boundaries and to the 4000-foot contour line.

ristic groups into seven classes on the basis of their main area of distribution relative to the study area. Introduced plants are not included in the tabulations.

All species which are reported to reach a distributional limit within the county are designated as range-terminating species.

The occurrence of each species in the nine major community types within the county was determined from field notes, herbarium specimens, and monographic sources.

It is assumed here that the occurrence of a species in a particular community type indicates something about its ecological amplitude and more specifically about the climatic tolerance of the species. That is, the characteristic and the dominant plants of each community type are considered to be indicators of climate. It seems better to use community type as a climate indicator rather than elevation, because of the effect of local modifying factors on the relationship between elevation and climate. It would be even better to monitor environmental factors directly, but this was logistically impossible.

In order to measure the degree of habitat specialization exhibited by various segments of the flora, a fidelity index is used:

$$FI = \frac{\frac{\text{total species in segment}}{\text{total community occurrences in segment}}}{\text{total species}} \div \frac{\text{total community occurrences}}{\text{total species}}$$

The values in this equation are derived in the following way. Each species in the flora occurs in one to nine possible community types. The value of the denominator equals the total species number (1067) divided by the total number of community occurrences (2182), or 0.489, indicating that the average species in the flora occurs in approximately two community types ($0.489 \approx \frac{1}{2}$).

The value for the numerator is derived in similar fashion, using total species number divided by total community occurrence

number for any subcategory or segment of the total flora. For example, the value of the numerator for the endemic class is 0.606 (83 species in segment divided by 137 total community occurrences).

The value of FI is defined as unity for the total flora, since in that case numerator and denominator have the same value. The value of FI for the endemic class would be 1.24 (0.606 divided by 0.489). Since this value is greater than unity, the endemic class shows a higher degree of habitat specialization than the flora as a whole. Values smaller than unity values would indicate the converse.

Given a value of 0.489 for the denominator, the value of FI can range from 0.23 (0.111 or one-ninth divided by 0.489) to 2.05 (unity divided by 0.489). These two extremes represent the respective cases of the average species in the segment occurring in all nine community types (one species/nine community occurrences) and in only one (one species/one community type).

Species which appear to be limited to a single substrate are designated as edaphically restricted species. Halophytes are not included in the edaphically restricted category because halomorphic soils develop on a variety of substrates.

FACTORS GOVERNING MIGRATION RATES

Propagule dispersal is a stochastic process. A plant disperses propagules in all directions, regardless of whether the propagule is likely to be dispersed to a site favorable for its growth, or whether an effective dispersal constitutes a range extension for the species.

An effective dispersal is accomplished when a propagule is dispersed to a site for which it is preadapted in terms of genetic tolerance (Good 1930) and is therefore able to grow and reproduce. When this site falls outside the previous distributional area for the species, the process is called migration.

Effective dispersal (and thus migration) is a function of three sets of variables. These

are distance, size of population supplying propagules, and time. Their operation is based simply on the laws of chance. The first two variables may be related to the third as an expression of rate. The rate at which a species is able to migrate is a function of effective source-population size and of average minimum dispersal distance (the average minimum distance a propagule must be dispersed in order to arrive at a site for which it is preadapted). The larger the effective source-population size and the shorter the average minimum dispersal distance, the higher the migration rate.

Populations adjacent to the area of potential colonization are more likely to disperse propagules into the area than those located at greater distances. Therefore, the rate of migration into an area is most influenced by properties of populations immediately adjacent to that area.

The size of effective source-population is conditioned by several factors: 1) absolute size and density of the population, 2) reproductive efficiency, and 3) dispersal efficiency. These simply say that the chance of propagules being dispersed to sites for which they are preadapted is increased if more propagules are produced and if propagules can disperse more efficiently.

Minimum dispersal distance is the same for all propagules produced by a population only when they are all preadapted to identical sites. More often, minimum dispersal distance is different for different propagules because of their preadaptation to different environments. The average minimum dispersal distance represents a mean value for all the propagules produced. It is dependent upon three sets of factors: 1) environmental heterogeneity, 2) amount of genetic heterogeneity for tolerance characters present in the population, and 3) degree of congruence between environment and tolerance characters of the dispersed propagules.

If the environment is homogeneous and favorable, the average minimum dispersal distance will be very short, and migration will be relatively rapid. If the environment

is homogeneous and unfavorable, the average minimum dispersal distance will be very long and migration will be relatively slow. Furthermore, these effects will increase with the degree of genetic homogeneity of the population.

Thus a population with narrow tolerance (low genetic heterogeneity) will be able to migrate rapidly through an environment which is homogeneous and favorable because of the very high probability that a propagule will be dispersed to a site for which it is preadapted. But its rate of migration through an environment which is homogeneous and unfavorable will approach zero, because of the very low probability that a propagule will be dispersed to a site for which it is preadapted.

A population with broad tolerances (high genetic heterogeneity) would be able to migrate less rapidly than a species with narrow tolerances through an environment which is homogeneous and favorable. This is because of the production of some propagules preadapted to conditions other than those present in the homogeneous environment. It would, however, be able to migrate more rapidly through a homogeneous and unfavorable environment. This is because it produces propagules preadapted to a wider variety of environments, and thus some propagules are likely to be preadapted for survival in the potential migration area.

A heterogeneous environment is made up of a mosaic of different environments. A genetically heterogeneous population will produce propagules preadapted to a wide range of environments, and thus a high proportion of the heterogeneous environment will be "read" as favorable by the average propagule it produces. This means that the average minimum dispersal distance will be relatively small and thus that migration will be relatively rapid.

A genetically homogeneous population will produce propagules preadapted to a narrow range of environments; hence a low proportion of the heterogeneous environment will be read as favorable. Average

minimum dispersal distance will be relatively large, and migration will be relatively slow.

This model is attractive in its simplicity but is lacking in several respects. Most importantly, it does not take into account the fact that both the genetic constitution of the population and the environment may themselves be changing through time. In effect, it is an instantaneous rate expression; it simply describes the options at a given point in time. In nature the situation is complicated by the fact that several of the variables in the rate expression may themselves be changing.

A change in the environment might change the configuration of favorable and unfavorable sites for a population and thus alter its migration rate. In some cases sites already occupied might become unfavorable, causing a diminution in range. Such secular climatic changes are well documented in the general area under discussion (Mehring 1965, Mehring and Martin 1965). It is important to consider that a species may have attained its modern distribution under environmental conditions very different from those now prevailing.

The genetic constitution of a population is subject to change from several sources. Two of these, gene flow and selection, are particularly important in this discussion. The former would tend to have the general effect of increasing heterogeneity. The latter could have one of three effects. In a homogeneous and constant environment, normalizing selection would tend to decrease variability. In a homogeneous but progressively changing environment, directional selection would tend to produce an adaptive shift, providing that the original population was sufficiently variable. In a spatially heterogeneous environment, disruptive selection could operate to produce genetically differentiated subpopulations, particularly if gene flow between subpopulations were minimized. These sources of genetic change are especially important in an area such as the one studied, which

meets the criteria of Stebbins (1974) for an area in which active speciation may be expected to be proceeding. It is also an area in which much of the habitat is hybrid-inducing in the sense of Anderson (1949). Many otherwise allopatric species have distributions which overlap in this area; they can often be observed to introgress or intergrade, depending on the viewpoint as to their origins.

In spite of the shortcomings of the model of migration rate presented above, it is quite useful in interpreting Washington County data.

DISCUSSION OF DATA

For interpretive purposes, two sorts of information about each species are examined. One involves the distribution pattern for the species as a whole. The other involves ecological factors which govern its distribution within the transition area. When these two sets of information are examined together, a high correlation between geographic distribution and particular ecological requirements becomes apparent.

Table 1 shows the percent contribution of each of seven distributional classes to the range-terminating group as compared to the total flora. It can be seen that the classes do not contribute equally to these two groups. The Mojave, Colorado Plateau, and endemic classes contribute far more than their share to the range-terminating group, making up almost 70 percent of this group but comprising only about 40 percent of the total flora. These differences are made up partially by the northern class, which is notably underrepresented in the range-terminating group.

Column three of Table 1 shows the percentage of species contained within each distributional class which are range-terminating. This value is almost 100 percent for the endemic and Mojave classes, indicating that a high proportion of the species may have reached a point which necessitates migration through an environment that is

homogeneous and unfavorable. This possibility is reinforced by the fact that they show high fidelity indices, indicating a high degree of habitat specialization and thus a low degree of genetic heterogeneity for climatic tolerance characters.

The Colorado Plateau and Great Basin classes also show a relatively high percent of range-terminating species, indicating a higher sensitivity to the environmental transition between the Colorado Plateau and the Great Basin than might have been expected. In fact, these two classes account for almost a third of all range-terminating species, a contribution almost as great as that of the Mojave class.

The southern class also shows a high proportion of range-terminating species, but the converse is true of the northern group. These apparently do not read the environment to the south of the county line as homogeneously unfavorable. One explanation for this is the fact that the northern class is not as specialized ($FI = < 1$) and thus should be able to migrate more effectively through a heterogeneous or even homogeneously unfavorable environment. Another possibility is that these species attained their distributions at some time in the past when environment was more homogeneously favorable.

The range-terminating members of the northern class have a much higher fidelity index than the class as a whole. These species would presumably have trouble mi-

grating through the heterogeneous environment of the transition zone because, due to their genetic homogeneity, they tend to read more of it as unfavorable. In fact, the range-terminating members of a class consistently show a higher fidelity index than the class as a whole, lending credence to the concept that low genetic variability for tolerance characters makes migration across a transition zone more difficult.

Table 2 shows the percentage contribution to each community type and to the total flora by each of the seven directional distribution classes. The community types are arranged roughly in altitudinal sequence.

The nondirectional class is slightly to markedly overrepresented in every community type except the Hot Desert Shrub community. In general, the species have broad tolerances and occur in a variety of community types, a fact also evidenced by their low fidelity index (0.79).

About 85 percent of the Mojave species occur in the Hot Desert Shrub community, making up almost half of the total flora. Perhaps more significant is the fact that an appreciable percent of the species in two of the higher elevation communities, Foothill Woodland (11 percent) and Mountain Brush (6 percent) is comprised of Mojave species. Bearing in mind that over 98 percent of the Mojave species are range-terminating, it is clear that some of these species (almost 20 percent of the total Mojave class) reach a

TABLE 1. Range termination and fidelity indices by directional class.

Directional Class	% Total Native Flora	% of Total Range-Terminating Species	% Range-Terminating Species in Class	Fidelity Index Total Class	Fidelity Index Range-Terminating Species
Endemic	7.8	14.0	96.4	1.24	1.24
Nondirectional	25.5	<1.0	<1.0	0.79	—
Mojave	17.6	32.3	98.4	1.32	1.34
Colorado Plateau	14.3	22.2	83.0	0.86	1.12
Great Basin	6.6	8.4	68.6	1.26	1.46
Northern	20.5	13.5	35.2	0.96	1.22
Southern	5.5	8.6	83.1	1.04	1.09
Anomalous	2.2	1.0	—	—	—
Total Flora	100.0	100.0	53.6	1.00	1.23

termination of range in spite of the fact that their tolerance characters permit some individuals to disperse successfully to higher elevation community types.

Most of the Mojave species have their main area of distribution in terms of numbers of individuals in the Hot Desert Shrub community. Their occasional anomalous occurrence in higher elevation community types indicates a broader climatic tolerance than that of species sharply restricted to the hot desert. Such species should be able to migrate through the ecotonal area because they can read at least some of it as favorable. Therefore, there seems to be no *a priori* reason for them to reach a limit of range in Washington County. Several factors might operate, however, to make their rate of further migration very slow.

Even though hot desert populations might be large, propagules preadapted for high elevation community types might be produced at very low frequencies. In addition, populations occurring in higher elevation communities might have lowered reproductive efficiency, thus retarding the establishment of large populations which could produce a higher frequency of preadapted propagules. Both factors would have the effect of keeping the effective source-population small.

The migrating species might be able to occupy only a portion of the sites within the higher-elevation vegetation types; the proportion of favorable sites might decrease with increasing distance from the transition zone. This could be true if the species were

only marginally tolerant climatically, if it had a narrow tolerance for some other environmental factor, or if it faced a competitive disadvantage in the presence of some high elevation species. All of these factors would have the effect of increasing the average minimum dispersal distance by increasing the proportion of unfavorable sites. Finally, the species may actually have migrated beyond the transition zone, but in such small numbers as to have escaped detection. In any case, the complex dynamics of the situation make it impossible to divide range-terminating species neatly into those which are limited by environmental factors and those which are not.

The community contributions of the remaining classes are easier to interpret. Since Rocky Mountain species enter the county via the Colorado Plateau, it is not surprising that the Colorado Plateau class is well represented in montane communities, particularly those of middle elevations. Many of these montane species reach a western limit of range, probably because of the much lower proportion of favorable sites and the much larger average minimum dispersal distances involved in migrating across the Great Basin. The class as a whole is underrepresented in Hot Desert communities, and most species which do occur there are not range-terminating. The important role played by edaphic factors in this class will be discussed later.

Very few of the Great Basin species enter the county at all; many reach southern and eastern range limits a few miles northwest

TABLE 2. Percent composition of plant communities by directional class.

Directional Class	% Total Native Flora	% Hot Desert	% Cold Desert	% Desert Riparian	% Foothill Woodland	% Mountain Brush	% Transition Forest	% Mountain Forest	% Mountain Riparian	% Mountain Meadow
Endemic	7.8	6.6	7.0	2.9	10.1	8.2	7.8	4.7	2.7	4.6
Nondirectional	25.5	16.2	34.9	39.4	31.2	33.7	37.0	33.2	40.5	31.8
Mojave	17.6	46.0	9.5	17.3	10.7	5.8	1.0	1.0	1.4	0
Colorado Plateau	14.3	9.2	14.0	9.0	15.8	17.3	21.9	15.8	12.2	12.1
Great Basin	6.6	6.6	7.0	5.1	6.4	5.8	2.7	5.3	3.2	1.0
Northern	20.5	4.0	18.1	14.4	15.4	23.1	25.1	37.9	36.9	50.5
Southern	5.5	9.0	7.0	9.4	6.7	3.4	2.7	1.0	1.4	0
Anomalous	2.2	2.3	2.5	2.5	3.7	2.9	1.8	2.1	1.8	0

of the county line. Those which do enter the county show a high degree of habitat specialization, but, oddly enough, this specialization is not to any particular community type. Classic Great Basin salt desert does not occur in Washington County, which may account for the disproportionately high representation of Great Basin species in other community types. Also, the total number of species is so small that a difference of a few species has a relatively large effect on the percent values.

As would be expected, species of the northern class are abundantly well represented in high montane communities, reasonably well represented in foothill communities, and poorly represented in desert communities.

Values for the southern class show the opposite relationship. They are poorly represented in montane communities and well represented in desert communities.

Members of the endemic class show a high degree of habitat specialization ($FI = 1.24$), and are overrepresented in relatively xeric communities at low and middle elevations. They are noticeably underrepresented in riparian communities. This may be because xeric environments tend to be more heterogeneous than mesic habitats in respect to variables other than moisture, and heterogeneous environments tend to restrict migration of specialized plant species, thus keeping them endemic.

Possible relationships between the areal extent of a distribution type and the ecological amplitude of the component species will now be explored. Table 3 gives fidelity index values and percent community composition for each of the five areal distribution classes. These show that a distribution type which covers a large area is more likely to include species with broad tolerances than a distribution type which covers a small area. The endemic and restricted classes show higher habitat specialization than the moderate class, which in turn shows a higher value than the wide class. This makes sense in light of the fact that species with broad tolerances should not only have more favorable sites available to them, but they should also be able to migrate more rapidly to occupy these sites.

An exception to this trend is exhibited by the continental + class, which contains a high proportion of transoceanic species. The community composition values for species of this class show that they are heavily concentrated in communities which provide aquatic habitat, and in fact many of these species are restricted to aquatic environments. They have probably been able to achieve wide distributions in spite of being habitat specialists by virtue of superior dispersal efficiency. It is these species which bring the index value for the Continental + group to a value which seems anomalously high.

TABLE 3. Fidelity indices, percent edaphically restricted species, and percent composition of plant communities by areal class.

	Endemic	Restricted	Moderate	Wide	Continental +
% Total Native Flora	7.8	27.5	16.8	33.0	12.8
Fidelity Index	1.24	1.25	1.00	0.83	1.01
% Edaphically Restricted Species	36.1	39.8	15.7	7.2	0
% Hot Desert Shrub	6.6	44.5	23.4	21.4	1.7
% Cold Desert Shrub	7.0	21.3	17.8	43.5	7.9
% Desert Riparian	2.9	17.0	17.3	37.5	22.7
% Foothill Woodland	10.1	20.1	21.5	40.3	4.4
% Mountain Brush	8.2	14.9	21.2	46.6	6.3
% Transition Forest	7.8	18.3	15.1	46.1	11.0
% Mountain Forest	4.7	19.5	8.9	45.3	19.5
% Mountain Riparian	2.7	13.1	5.9	44.6	32.0
% Mountain Meadow	4.6	12.1	11.2	49.5	22.4

Plants of wide but subcontinental distributions do not show this specialization, but instead are well represented in all but the Hot Desert Shrub community type. Plants of moderate distribution tend to be better represented in the lower-elevation communities. The trend continues in the group of restricted distribution, which is relatively underrepresented in all but the Hot Desert Shrub community type. This trend seems to indicate that groups of wider distribution show higher percentages in mesic types, while groups of narrower distribution show higher percentages in xeric types. This makes sense in view of the relative proportion of mesic to xeric environments in the world, on the continent, in the West, and in the intermountain-southwestern area, respectively. The values for the endemic class have been discussed above.

The importance of edaphic factors in the transition area will be examined next. Tolerance for edaphic factors, like tolerance for other environmental factors, is a matter of degree. This discussion takes into account only those species which have a very narrow edaphic requirement. Even though these make up only about 8 percent of the total flora, the implication that edaphic factors play a minor role in the transition area is not warranted. Many more species show some degree of edaphic specialization, and as noted above, distributional limits are not all or nothing propositions based on pres-

ence or absence of adaptive traits, but instead are also a matter of degree. The patterns for the sharply restricted species seem to indicate that edaphics may be more important in the transition area than might be supposed.

Table 4 shows the percentage of all species versus the percentage of edaphically restricted species occurring in each community type. Though both these values tend to decrease with an increase in altitude, edaphically restricted species drop much more sharply. In addition, this group is poorly represented in the Desert Riparian community. Clearly edaphically restricted species are much better represented in xeric than in mesic community types. This may indicate that the environment is more heterogeneous edaphically in dry than in wetter environments. Mesic soils developed on different substrates tend to be more modified and more alike than xeric soils developed on those different substrates.

A consequence of such environmental heterogeneity is that edaphically restricted species tend to belong to more restricted areal distribution types. This is because species with narrow edaphic tolerances migrate slowly through an edaphically heterogeneous area. It may also be because the substrate itself is of restricted geographic occurrence. The first and third rows of Table 3 demonstrate this relationship.

An edaphically restricted species will be able to migrate relatively rapidly in spite of low genetic heterogeneity as long as the environment is homogeneous and favorable in terms of substrate. When such a species reaches a range limit, it is probably because it has reached a point where the substrate environment suddenly becomes very heterogeneous or homogeneous and unfavorable. The favorable substrate may occur at widely spaced sites of small areal extent instead of closely spaced sites of large areal extent, or it may be completely absent from the potential area. In any case, the average minimum dispersal distance becomes prohi-

TABLE 4. Percentage of all native species and of all edaphically restricted species occurring in each plant community.

Plant Community	% Total Native Species	% Edaphically Restricted Species
Hot Desert Shrub	32.4	63.9
Cold Desert Shrub	29.5	37.3
Desert Riparian	26.0	13.3
Foothill Woodland	27.9	32.5
Mountain Brush	19.5	15.7
Transition Forest	20.5	12.1
Mountain Forest	17.8	2.4
Mountain Riparian	20.8	2.4
Mountain Meadow	10.0	1.2

bitively large, and migration slows to near zero.

Table 5 shows the substrate preferences of edaphically restricted species belonging to each of the seven directional distribution classes. The northern class contributes no edaphically restricted species. This is not surprising in view of the high preference of this group for mesic environments, which do not promote edaphic specialization.

The nondirectional class contributes only one limestone-restricted and one sandstone-restricted species, and as a group is markedly underrepresented. The southern class and the Great Basin class are also slightly underrepresented and contribute only a handful of the edaphically restricted species. This means that most of these species must be contributed by the remaining three classes.

Over a quarter of the species are contributed by the Mojave class, but these are distributed very unevenly among the substrates. Mojave species constitute almost two-thirds of the limestone-restricted class, about one-fourth of the sand-restricted class, and less than 10 percent to the remaining classes.

The Colorado Plateau class accounts for almost a third of the total. But, in contrast to the Mojave class, none of these are limestone-restricted. Instead they make up almost two-fifths of the sandstone-restricted species, one-fifth of the clay-restricted species, and about two-thirds of the sand-restricted species.

The endemic class accounts for the remaining third of the total. This class contributes the only volcanic-restricted species, about three-quarters of the clay-restricted species, and two-thirds of the sandstone-restricted species. None of the endemics are sand restricted.

Over 90 percent of the edaphically restricted species are range-terminating. The role of substrate specialization as a factor in range-termination seems clear. Limestone-restricted species appear to migrate rapidly across the southern Basin and Range Province, but their rate of migration nears zero when they encounter the sandstones and shales of the Colorado Plateau. Conversely, sandstone- and clay-restricted species seem to migrate rapidly across the Colorado Plateau, but their rate of migration nears zero when they encounter the high-carbonate soils of the Basin and Range Province. Sand is a substrate which is widespread, especially in the Colorado Plateau Province; thus sand-restricted species do not tend to be endemics. But there is sand in the Mojave Desert; thus some sand-restricted species enter the county via the Mojave. These may be prevented from migrating further north by other than edaphic factors.

SUMMARY

The data show that the high proportion of range-terminating species in the county flora is correlated with the abrupt shifts

TABLE 5. Edaphically restricted species by substrate and directional class.

Directional Class	% Total Native Flora	% Edaphically Restricted Group	% Volcanic-Restricted Species	% Sand-Restricted Species	% Sandstone-Restricted Species	% Limestone-Restricted Species	% Clay-Restricted Species
Endemic	7.8	36.1	100.0	0	62.5	15.8	69.6
Nondirectional	25.5	2.4	0	0	0	10.6	0
Mojave	17.6	24.0	0	25.0	0	63.2	8.7
Colorado Plateau	14.3	28.9	0	54.2	37.5	0	21.7
Great Basin	6.6	3.6	0	8.3	0	5.2	0
Northern	20.5	0	0	0	0	0	0
Southern	5.5	3.6	0	8.3	0	5.2	0
Anamalous	2.2	1.2	0	4.2	0	0	0
Total Species	100.0	100.0	100.0	100.0	100.0	100.0	100.0
% Total Edaphically Restricted Species	—	—	1.2	28.9	19.3	22.9	27.7

along environmental gradients oriented in north-south and in east-west directions. The north-south gradient is primarily climatic, while the east-west gradient is both climatic and edaphic.

Species with narrower tolerances are shown to be more sensitive to these abrupt environmental shifts. It is also shown that some of the range-terminating species have the capacity to migrate beyond the transition zone under present conditions, but that differences in relative migration rates give their distributional limits within the county a quasi-stable aspect.

CONCLUSION

Just about anything is statistically possible in biogeography. This makes it dangerous to conclude that any species has a migration rate of zero. It is possible for a propagule to be dispersed to a tiny enclave of favorable environment in the midst of a vast area of homogeneous and unfavorable environment. And it is possible that the very rare propagule which has tolerance characters near an extreme for the species will be dispersed to a site for which it is pre-adapted. These events may be very unlikely, but they are possible. They may result in some of the seemingly aberrant "dots" often seen on species distribution maps.

Instead of considering only two possibilities, those species which are environment-limited in their current distribution pattern and those which are not, it seems far better to consider these two possibilities as extremes on a continuum. This involves recognition of the interplay among a complex series of factors which interact to produce the probability that a species will be able to migrate at a given rate under a given set of conditions. These concepts may prove difficult to tie down, but it is hoped the ideas presented here will facilitate the process—if they only begin to sharpen the focus on this complex and interesting problem.

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